Giraffe social preferences are context dependent

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The dynamic nature of animal societies often hides multiple layers of complexity. The field of animal behaviour is rapidly advancing with the development of increasingly sophisticated analytical methods that allow scientists to identify complex and nuanced drivers of social patterns. The resurgent interest in giraffe sociality illustrates this by challenging the early view that individuals interact at random; it became clear that, instead, giraffes can be organized into multilevel societies, apparently founded on preferred associations. However, it is unclear whether such enduring associations result from active choice for specific individuals. The extent to which other social and asocial factors can contribute to an individual's inclusion in groups remains underexplored. Here we assess how context affects social preferences at the individual level by evaluating grouping patterns of giraffes in different behavioural states, habitats and levels of disturbance. When we controlled for potential class-based (as opposed to individual-based) assortment of individuals by sex, age and gregariousness, we found that giraffes only exhibited individual social preferences when foraging, with minor influence of habitat complexity or level of disturbance. Our results indicate that behavioural context is a major driver of giraffe social association. This strengthens recent evidence of complex social systems in giraffes and suggests that classic metrics of social relationships (such as association indices) may be too coarse, concealing true social preferences in wild populations.

Keywords:

association index

behavioural state

habitat complexity

Rothschild's giraffe

social affiliation

social network

social structure

The ways in which individuals interact with each other and their environment influence key population processes, including transmission of disease and parasites (MacIntosh et al., 2012; VanderWaal, Atwill, Isbell, & McCowan, 2014), information (Whitehead & Lusseau, 2012) and gene flow (Brent et al., 2013; Slatkin, 1987). Social interactions also have an impact on the most crucial aspects of individuals' lives—from health to fitness—since reducing risks and increasing access to resources are fundamental drivers for being social (e.g. Krause & Ruxton, 2002). Our study dissects the drivers of social interaction in the giraffe, *Giraffa camelopardalis rothschildi*, a social species with fluid but nonrandom patterns of association. We seek to distinguish the prevalence and context of individual preferences, as opposed to grouping based on age or sex, or passive effects of habitat.

While individuals can, and often do, interact with many conspecifics throughout their lives, it is the nonrandom, repeated interactions with certain individuals that are the foundation of social relationships (Hinde, 1976). Lasting, preferred relationships are among the social strategies that can improve individual fitness and survival. For example, stable male coalitions increase mating chances of bottlenose dolphins, *Tursiops* cf. *aduncus* (Connor & Krützen, 2015) and help chimpanzees, *Pan troglodytes,* to sire more offspring and climb the social ladder (Gilby et al., 2013; Silk, 2007a); the number of close associations held by savannah baboon, *Papio cynocephalus,* mothers directly relates to their infant's survival (Silk, Alberts, & Altmann, 2003); the number and strength of male–female bonds increase birth and offspring survival in wild horses, *Equus caballus* (Cameron, Setsaas, & Linklater, 2009), and life span in bottlenose dolphins (Stanton & Mann, 2012); and the strong mother–son bonds in the natal philopatric groups of killer whales, *Orcinus orca,* promote offspring survival (Brent et al., 2015). Despite such clear benefits of enduring social relationships, inherent costs of sociality can make social

interactions responsive and adaptive; this is particularly evident in societies with fission–fusion dynamics, where groups continually form and disband as individuals seek to balance the costs and benefits of group living (Aureli et al., 2008; Couzin & Laidre, 2009; Smith, Kolowski, Graham, Dawes, & Holekamp, 2008).

In these societies, social patterns result from multiple and dynamic factors, many of which can confound the identification of social preferences and their underlying motivations. For example, individuals can vary in gregariousness and be more or less prone to form groups (e.g. Godde, Humbert, Côté, Réale, & Whitehead, 2013), or be predisposed to assort with kin, or with individuals who behave similarly, or are of the same sex or age (Lusseau & Newman, 2004; Massen & Koski, 2014; Silk, 2002). Simultaneously, purely asocial factors such as demographic changes, range overlap and habitat structure can assemble or separate individuals in time and space (Cantor et al., 2012; Webber & Vander Wal, 2018), thereby defining the opportunities to interact socially. External biotic factors, such as habitat type and complexity, the distribution of resources, predation risk and competition or familiarity with conspecifics, can influence the spatiotemporal distribution of animals, thereby exerting external constraints on how they associate (Leu, Farine, Wey, Sih, & Bull, 2016; Morris, 2011; Smith et al., 2008; van Beest et al., 2014).

Fission–fusion dynamics arise through individuals adapting their social choices to maximize fitness (Farine, Montiglio, & Spiegel, 2015; Silk, 2007b). For example, the association patterns of adult male African elephants, *Loxodonta africana,* change with sexual status: sexually inactive adult males associate with conspecifics of a similar age, but when they are sexually active they associate with others of a wider age range (Evans & Harris, 2008; Goldenberg, de Silva, Rasmussen, Douglas-Hamilton, & Wittemyer, 2014). Bottlenose dolphins' preferred

associations are context dependent (Gero, Bejder, Whitehead, Mann, & Connor, 2005; Moreno & Acevedo-Gutiérrez, 2016) and can dissolve during foraging (Gazda, Iyer, Killingback, Connor, & Brault, 2015), and spotted hyaena, *Crocuta crocuta,* adjust their social behaviour to reduce interindividual conflict, infanticide risk and foraging competition (Smith et al., 2008). Beyond maximizing individual fitness, social choices and the resulting association patterns are linked to individual characteristics (Silk et al., 2009; Strandburg-Peshkin, Farine, Crofoot, & Couzin, 2017), spatiotemporal factors (Naud et al., 2016; Webber & Vander Wal, 2018) and behavioural state (Goldenberg et al., 2014; Moreno & Acevedo-Gutiérrez, 2016). If we are to reveal and understand true social preferences, it is important that factors extraneous to social relationships can be quantified and accounted for to understand their relative contribution or influence over social decisions (Moreno & Acevedo-Gutiérrez, 2016; Whitehead & James, 2015). Given the multifarious influence of biotic and abiotic factors on sociality, identifying their relative contribution remains a timely challenge (Farine & Whitehead, 2015; Pinter-Wollman et al., 2013; Whitehead & James, 2015).

Giraffes provide a good model system for examining the influence of behavioural context on patterns of social preferences due to the conspicuousness of their behaviours, the reliability in identification of individuals (Muller, 2018) and frequent changes in group membership. The resurgent interest in the fission–fusion social dynamics of giraffes has challenged the early portrayal of their social structure as random and unstructured (Dagg & Foster, 1976; Foster & Dagg, 1972; Le Pendu, Ciofolo, & Gosser, 2000; Leuthold, 1979). Recent work has shown how giraffes can be socially organized in multilevel societies (Horová, Brandlová, & Gloneková, 2015; VanderWaal, Wang, McCowan, Fushing, & Isbell, 2014) and engage in socially complex behaviours (Bashaw, Bloomsmith, Maple, & Bercovitch, 2007; Bercovitch & Berry, 2013;

Carter, Brand, Carter, Shorrocks, & Goldizen, 2013; Horová et al., 2015; Malyjurkova, Hejzlarova, Vymyslicka, & Brandlova, 2014; Pratt & Anderson, 1985; Shorrocks & Croft, 2009). For instance, giraffes maintain nonrandom preferred and avoided associations, which partially reflect patterns of genetic relatedness, home range overlap and individual preferences (Bercovitch & Berry, 2013; Carter, Seddon, Frère, Carter, & Goldizen, 2013). They also alter their social behaviour according to sex (Cameron et al., 2009), age (Bercovitch & Berry, 2015) and environmental conditions (Gloneková, Vymyslická, Žáčková, & Brandlová, 2017).

Our goal here was to assess how context affects social preferences at the individual level by evaluating grouping patterns of giraffes in different behavioural states, levels of habitat complexity and disturbance. Our overarching prediction was that social patterns in giraffes would be structurally different across activities and/or habitat settings; therefore, social preferences would only be revealed in certain contexts and after the removal of covariates that may affect the propensity to aggregate per se, irrespective of others' identities. We first quantified the extent to which a widely used measure of social relationship (association index) is dependent on behavioural state and habitat complexity. Then we tested whether individuals from two populations exposed to distinct levels of disturbance have social preferences after controlling for underlying mechanisms that may bring them together, such as assortative mixing by sex, age and gregariousness during different behavioural activities. We predicted that, if giraffes alter social association patterns to maximize fitness, then individuals would show weaker associations during foraging to avoid competition for resources (Smith et al., 2008) or in more complex habitats that may segregate individuals, but that they would show greater associative behaviour when travelling or resting, especially in more open habitats, to increase protection from predators (Lima, 1995; Lima & Dill, 1990).

<H1>METHODS

<H2>Study Areas

We carried out the study in the Great Rift Valley of Kenya, where the regional climate is dry sub-humid to semi-arid (Nicholson, 1996). Giraffe distribution in this region is fragmented and populations only exists within confined conservation areas (Brenneman, Bagine, Brown, Ndetei, & Louis, 2009; Muller et al., 2016). We compared two discrete, closed populations of Rothschild's giraffes in enclosed conservation areas: the Soysambu Conservancy (SC) and the Lake Nakuru National Park (LNNP). Both areas are part of the same biome and are separated by an electrified game fence that prevents the movement of large mammals; the shared boundaries run for 7.8 km along the southeastern boundary of LNNP and the western boundary of SC. SC is a 190 km^2 privately owned wildlife conservancy, which includes part of Lake Elementeita (00°46'S, 036°23'E; 1670 m above sea level). LNNP is a 188 km^2 National Park surrounding Lake Nakuru (0°22'S, 36°05'E; 1759 m above sea level). The habitat in both areas consists of large patches of *Acacia* species and mixed woodland interspersed with open savannah grassland.

There are two notable differences between the study sites: (1) the density of lions, *Panthera leo,* and (2) the levels of human activity. Lions are the only predator to pose a significant threat to giraffes (Dagg & Foster, 1976; Foster & Dagg, 1972; Hirst, 1969; Pienaar, 1969; Strauss & Packer, 2013). At the time of this study, LNNP contained 56 lions (Ogutu, Owen-Smith, Piepho, Kuloba, & Edebe, 2012), which is a high density (0.3 lion/km^2) compared to more typical densities of 0.08 to 0.14 lion/km^2 (Creel & Creel, 1997; East, 1984). Preferential

preying of lions upon giraffes has been identified as a problem in LNNP, along with observations of lions feeding on juvenile giraffe carcasses in the park (Brenneman et al., 2009; Kenya Wildlife Service, 2002). During the same time, SC was free of lions and had been for several decades (Hugh George Cholmondeley, owner of Soysambu Ranch, personal communication). Additionally, the levels of human-related disturbance also varied between sites; LNNP is one of Kenya's premier tourist destinations (Maingi, Ondigi, & Wadawi, 2016) and received 253 500 visitors in 2012 (Muthoka, Oloko, & Obonyo, 2017). In contrast, SC was free of tourism at the time of this study (Kenya Wildlife Service, 2004). To acknowledge differences in predator density and levels of human activity between sites, and because we could not discriminate between effects of predation and human disturbance with only these two populations, we used more general descriptions of 'lower disturbance' for SC and 'higher disturbance' for LNNP. We accept that we were unable to quantify predation risk in each population, but human-related disturbance can be considered a form of predation risk (Frid & Dill, 2002; Geffroy, Samia, Bessa, & Blumstein, 2015). Furthermore, high levels of human activity have been shown to alter the structure of networks (Belton, Cameron, & Dalerum, 2018), which supports our decision to refer to the two populations in terms of varying levels of disturbance.

<H2>Data Sampling

We first carried out a 3-month pilot study in each site to identify, sex and age all individuals. We also used this time period to determine a distance threshold at which giraffes could be approached by vehicle without our presence causing a change in behaviour, and took care to respect this threshold during data collection. Then we collected our data systematically

during a 9-month period in each study site (SC: May 2010–January 2011; LNNP: May 2011–January 2012) to reduce potential demographic and spatiotemporal biases in the giraffes' association patterns. We collected behavioural and photo-identification data while driving a 4×4 vehicle at 20 km/h along predefined routes through each study site to search for groups of giraffes. We split each study site into four blocks and surveyed all of them each day in a randomized order between sunrise at 0630 hours and sunset at 1830 hours (UTC + 3 h Standard Time). The definition of a giraffe 'group' is variable in the literature. During the pilot phase we determined that a distance of 1 km was an appropriate criterion for identifying a group, since groups were self-defining; the proximity of individuals within a group was typically up to 200 m, but intergroup distances were always above 1 km. We aimed to photograph and identify every giraffe in a group using a Nikon D90 digital SLR camera with an 18–200 mm Nikkor DX lens (Nikon Corp., Tokyo, Japan), and a 50–500 mm Sigma lens (Sigma Corp., Kawasaki, Japan). We sampled each group for exactly 30 min to standardize observation time between groups, and categorized each data point using a 'reliability score' that ranged from 1 to 3 (1: certain that all group members had been observed; 2: unsure whether all group members had been observed; 3: certain that all group members had not been observed). Only data points of score 1 were used in the analyses to ensure complete accuracy of identifications of group membership. Data reliability score was not influenced by habitat type or complexity; there were equal proportions of data points for each.

<H2>Individual Covariates: Sex and Age

We sexed and aged all individual giraffes visually (complete methodology in Muller,

2018). Accurate age classification of wild giraffes is difficult without the date of birth, but age classes are widely used as reliable alternatives (Foster, 1966; Foster & Dagg, 1972; van der Jeugd & Prins, 2000; Le Pendu et al., 2000; Pratt & Anderson, 1979, 1985; Young & Isbell, 1991). We defined four age classes: juvenile (<12 months), subadult (12 months to <4 years), adult (>4 years) and big bulls (mature adult males with dark coats and skull nodules, estimated to be ≥9 years old) (Berry & Bercovitch, 2012; van der Jeugd & Prins, 2000; Pellew, 1984; Pratt & Anderson, 1985).

<H2>Context-dependent Associations: Behavioural States and Habitat Complexities

To assess how context can affect social preferences, we quantified dyadic associations in each population from observations of grouped giraffes in three behavioural states and three levels of habitat complexity. We recorded the group's general behaviour as one of three main categories: forage, travel and rest. Forage was defined as the individuals engaging in a food intake activity, i.e. browsing or ruminating. Travel was defined as individuals moving between locations with purpose and direction. Thus, we classified individuals moving between trees to feed as 'forage', whereas we classified individuals walking from one location to another in a directed manner as 'travel'. Rest was defined as individuals standing still or sitting with the body at rest and not undertaking any browsing, ruminating, socializing or travelling activity. We found that individuals in groups synchronized their behaviour and typically remained in the same behaviour for the duration of our 30 min observation period. In cases where group members were engaged in different behaviours, we chose a category that reflected the behaviour of most group members. Where group behaviour changed during the observation period, the observation and

the data record were excluded from the analysis.

To define levels of habitat complexity, we first characterized habitats by general physiognomy. *Acacia* woodland was any wooded area comprising >85% *Acacia* species. Mixed woodland was any wooded area comprising <85% *Acacia* species, and typically contained mixed tree and shrub species including *Euphorbia* spp., *Acacia* spp. and *Olea africana* (Mutangah, 1994). Open plain was any open savannah or grassland area. We then scored each habitat for three-dimensional complexity based on openness categories: (1) low complexity (0–10% tree or shrub cover); (2) medium (10–50% tree or shrub cover); and (3) high complexity (50–100% tree or shrub cover). Since habitat type and complexity are not independent measures, we used only habitat complexity in our analyses.

We then quantified dyadic associations in each behavioural state and in each habitat complexity. We defined association between individuals based on group membership, that is, individuals observed in the same group within a daily sampling period were considered associated ('gambit of the group'; Whitehead & Dufault, 1999). From a binary group-by-individual matrix, we calculated the half-weight association index (HWI, Cairns & Schwager, 1987) to quantify the proportion of time a pair of individuals were observed together in relation to the time that they were observed apart as:

$$\mathrm{HWI} = \frac{x}{x + y_{\mathrm{AB}} + \frac{1}{2(y_{\mathrm{A}} + y_{\mathrm{B}})}}$$

where x is the number of daily sampling periods that individuals A and B were observed in the same group; y_{A} and y_{B} are the numbers of sampling periods in which only A and only B, respectively, were identified; y_{AB} is the number of sampling periods in which A and B were

identified separately (Whitehead, 2008). In each population's association matrices, a cell denoted the association between the *i*th and *j*th individuals that were observed more than five times (Bercovitch & Berry, 2015; Croft, James, & Krause, 2008). To create context-dependent association matrices, we took all individuals seen in all behavioural states and in all habitat complexities and recalculated their half-weight association indices in each behavioural state—HWI(forage), HWI(travel), HWI(rest)— and in each complexity level—HWI(low), HWI(medium), HWI(high).

<H2>Influence of Structural Variables on Dyadic Associations

To assess the extent to which associations between individuals were influenced by the context and individual covariates, we built matrix regression models with the multiple regression quadratic assignment procedure (MRQAP; Dekker, Krackhardt, & Snijders, 2007; Krackhardt, 1988). MRQAP tests for relationships between a matrix representing a given dyadic dependent variable (here, HWI associations) and multiple matrices representing dependent structural variables (see below), while controlling for the effect of each of them. We used the double semi-partialling technique (Dekker et al., 2007), which uses Monte Carlo methods to permute randomly the residuals of the model (1000 iterations) and so avoid potential autocorrelation between the relational data in the dependent association matrix and the other matrices. As effect size statistics, we used partial correlation coefficients between the dependent and each independent matrix (Farine & Whitehead, 2015).

We first tested the combined effect of all variables (individual covariates, behavioural-dependent associations, habitat complexity-dependent associations) on the dyadic associations

defined by group membership. To do this, we created two full MRQAP models for each population (Appendix Table A1). In each model the dependent variable was the HWI association matrix among all individuals that were observed in all three behavioural states (or in all three habitat complexity levels), and the independent structural variables were the context-dependent associations matrices described earlier, and matrices describing gregariousness, sex and age classes as follows.

Gregariousness was defined as the tendency of individuals to be consistently found in larger or smaller groups (Whitehead, 2008). Since this tendency can bias the estimates of dyadic social relationships measured by association indices, we corrected the association indices of all dyads by gregariousness based on the expected values of the index, given the estimated gregariousness of the individuals (Godde et al., 2013). To use gregariousness as a structural variable, we needed to remove the circularity, in that a high association index between individuals *i* and *j* increases their joint gregariousness, by omitting the association index of *i* and *j* when calculating gregariousness by summing all HWI for *i* except the HWI_{ij}, and multiplying it by the sum of all HWI for *j* except HWI_{ji} (Whitehead & James, 2015):

$x(\text{gregariousness})_{ij} = \log\left(\sum_{k\neq i,j} \text{HWI}_{ik} \times \sum_{k\neq i,j} \text{HWI}_{ik}\right)$, where HWI is their association index. To depict the dyadic relationships of the categorical variables sex (female or male) and age (juvenile, subadult, adult, big bull) as structural variables, we built binary matrices in which elements $a_{ij} = 1$ when individuals *i* and *j* were of the same category (e.g. both female or both adults) and $a_{ij} = 0$ otherwise (e.g. *i* is female and *j* is male; *i* is adult and *j* is juvenile).

<H2>Removing Confounding Factors in Social Preferences

We built generalized affiliation indices (GAI) to assess social affiliations, that is, active association preferences among individuals (Whitehead & James, 2015). GAIs remove the contributions, if any, of multiple structural causes of group-based associations and extract the social preference of individuals consistently observed in close proximity (see Whitehead & James, 2015). Formally, GAIs are the residuals of a generalized linear model in which the dependent variable is a social relationship metric (here, the HWI), and the independent variables are structural variables that can confound the reason why individuals get together in groups (Whitehead & James, 2015). In other words, GAI represents the variance that is not explained by assortativity of individuals due to these structural variables. Biologically, the GAI is a more refined representation of social affiliations (individuals actively preferring to get together in groups) than the association index (Whitehead & James, 2015).

We created a GAI for each behavioural state separately (forage, travel, rest) and combined (all behaviours), and similarly for each habitat complexity (low, medium, high, all), totalling eight GAIs for each of the two populations. The dependent variables were a context-dependent half-weight association matrix as explained above (e.g. HWI for all foraging individuals, for all groups in low complex habitat, etc.). In all cases, we used the matrices representing three individual covariates (sex, age, gregariousness) as independent variables. To select the significant independent variables in each case, we first ran a MRQAP to test whether the association matrices were significantly correlated with these individual variables. That is, we first tested whether individuals of similar gregariousness, or of the same sex or age class, have higher association indices (Appendix Table A2). Then we retained only the significant independent variables in each MRQAP test to build the corresponding GAI (Appendix Table A3). All GAIs were created assuming binomial distribution, which is appropriate for

proportional association measures such as the HWI (Whitehead & James, 2015).

Since GAIs are residuals of a linear model, these can take either positive or negative values; we used the deviance residual transformation so they would become approximately normally distributed, with mean ~0 and standard deviation (SD) ~1. This transformation makes particularly high and low residuals more easily identifiable: residual deviance GAI >2.0 suggests high social affiliation or preference, while GAI <-2.0 suggests social avoidance (Whitehead & James, 2015). To compare visually the distribution of GAI across all contexts, we fitted a probability density function using the kernel density estimation to the upper triangle of each symmetrical GAI matrix. We then used two-sample Kolmogorov–Smirnov analysis to test the maximum distance between the distributions of GAI considering all behavioural states and the distribution of GAI in each behavioural state; similarly, we compared the distribution of GAI considering all habitat complexities with the GAI of each habitat complexity level. In these two-tailed tests with $\alpha = 0.05$, the null hypothesis was that the distance between the GAI distribution considering all data and the distribution of a context-dependent GAI was not greater than the distance if they were drawn from the same distribution.

<H2>Testing for Social Affiliations

We performed Monte Carlo permutations to test whether there were indeed unusually high and low affiliations in each behavioural and habitat context. We tested the overarching null hypothesis of random social affiliations against the alternative that pairs of individuals have avoided or preferred associations (Bejder, Fletcher, & Bräger, 1998). We permuted dyads of individuals observed during the same day (i.e. a sampling period) 1000 times (with 1000 flips

each) using a swapping algorithm (Bejder et al., 1998). We permuted all the raw observed data of individuals into groups, within daily sampling periods to remove demographic effects (Whitehead, 2008); at each iteration we recreated the corresponding GAI model to build a randomized affiliation matrix to which we compared two summary statistics (mean and SD) with the observed GAIs. We considered preferred and avoided social associations to exist among pairs of individuals between daily sampling periods when the SD of the observed GAI was higher than the SD expected by chance (Bejder et al., 1998; Whitehead, 2008; Whitehead & James, 2015). We also evaluated potential social preferences within daily sampling periods by checking whether the observed mean of the GAI was lower than the average mean GAI of all permuted replicates (Whitehead, 2008).

<H2>Social Affiliation Networks

We used the network approach to visualize the context-dependent social affiliations (Farine & Whitehead, 2015). We used GAI as the adjacency matrices of context-dependent social networks, in which each cell denoted the affiliation between the *i*th and *j*th giraffe as indicated by the deviance residuals of the corresponding GAI model. In the undirected weighted network depiction, nodes representing individuals were differentiated by sex (shape), age (colour) and gregariousness (size) and connected by edges whose thicknesses were proportional to the GAI values. Since we were interested in the social preferences, we filtered the networks to only plot the GAI values >2.0 (Whitehead & James, 2015).

To compare network patterns, we calculated two global metrics—connectance and assortativity coefficient—which are independent of network size and so comparable across the

different behavioural states, habitat complexities and populations. The connectance of a social network measures social connectivity as the proportion of realized edges in relation to all possible edges as $C = \frac{2L}{n \cdot (n-1)}$, where L is number of observed links and n is number of nodes (e.g. Croft et al., 2008). The assortativity coefficient measures whether edges in a network typically occur between similar or dissimilar nodes, and was used here to infer the tendency for individuals of the same sex, age or gregariousness to display high affiliations across the different contexts. We calculated weighted assortativity indices (Farine, 2014), which range from -1 (a fully disassorted network) to +1 (a fully assorted network). We used the discrete index, r_d^w, for sex and age classes, and the continuous index, r_c^w, for gregariousness, estimating their standard errors (SE) through jackknife procedures (Farine, 2014).

<H2>Ethical Note

Our study was noninvasive and exclusively observational, carried out with the permission of the Kenya Wildlife Service and the Kenya National Council for Science and Technology (permit NCST/RRI/12/1/MAS/08/5) and approved by the University of Bristol Ethics Committee (project number UB/11/003). All giraffes in both populations were habituated to the presence of vehicles and were free to exhibit natural behaviour. Nevertheless, we were careful to minimize disturbance by approaching giraffes slowly, always stopping the research vehicle at a distance so as not to disturb their natural behaviour or cause any stress. Consequently, giraffes did not move away from our research vehicle or appear disturbed by our presence.

<H2>Data Accessibility

All analyses were carried out, and can be reproduced, in the open-source Socprog 2.7 programs (Whitehead, 2009). All data will be made available by the authors upon request.

<H1>RESULTS

In the population under lower disturbance level (SC), we observed a total of 77 giraffes, 55 of which performed the three behavioural states (31 females, 24 males, 16 juveniles and the rest were adults and subadults) and 65 of which used all three levels of habitat complexity (32 females, 33 males). These figures were similar in the population under higher disturbance (LNNP), where 45 of the 89 individuals (19 females, 26 males; all adults and subadults) were observed performing the three behavioural states and 76 of the 89 individuals (40 females, 36 males; all adults and subadults) were seen in all levels of habitat complexity. In the further analyses, we considered only such individuals that were observed in all behavioural states and habitat complexities (see Appendix Table A4).

In both populations, the all-inclusive association indices (HWI) were strongly correlated with the context-dependent associations (the complete results of the full MRQAP models are given in Appendix Table A1). That is, the associations quantified for all behavioural states combined were highly correlated with the associations for each behavioural state (partial correlations ranging from 0.59 during travel to 0.96 during forage); likewise, the associations for all habitats combined were highly correlated with the association in each habitat complexity level (from 0.76 in low to 0.93 in medium complexity). When we broke down these analyses to each behavioural state and habitat complexity level (complete results in Appendix Table A2), we

found that the associations in each state and level were influenced by the individual covariates age, sex and gregariousness. However, age was not a strong influencing factor in the population under higher disturbance (LNNP), where individuals seemed to associate with others without discriminating based on age class (but note the absence of juveniles in the analyses for LNNP; Appendix Table A4), suggesting that population structure also influenced social organization.

Density distributions of GAI, considering all behavioural states and all habitat complexities, tended to be bell-shaped (Fig. 1). However, when we separated the GAI in each of the three behavioural states and habitat complexity levels, these context-dependent affiliation indices tended to a bimodal distribution (Fig. 1). This suggests that giraffes alter their associations dependent upon group behavioural state and habitat complexity, and that accounting for context can differentiate more discrete sets of high or low affiliations. Furthermore, the density distributions of GAI values considering data from all behavioural contexts resembled the GAI distribution during foraging in both giraffe populations (SC: $D = 0.012$, $P = 0.999$; LNNP: $D = 0.076$, $P = 0.103$), but were different than the GAI distributions during travel and rest (Fig. 1a, b; full Kolmogorov–Smirnov tests in Appendix Table A5). The density distribution of GAI values considering all habitat complexities combined was more similar to the distribution of GAIs when individuals were in habitats of medium complexity (SC: $D = 0.068$, $P = 0.183$; LNNP: $D = 0.098$, $P = 0.015$) and distinct from the GAI distributions when in low and high complexity levels (Fig. 1c, d, Appendix Table A5).

Notably, for both populations the coarse association index (HWI) suggested social preferences among individuals in all habitat complexity levels and during all behavioural contexts, whether for preferences within days (see mean HWI, Appendix Table A3) or between days (see SD HWI, Appendix Table A3, Fig. 2). However, refined social metrics (i.e. GAI,

removing effects of individual covariates and separated by behavioural and habitat contexts) indicated that (1) social preferences occurred mostly between days, (2) when we controlled for behavioural context, social preferences only emerged during forage, but not during travel or rest (Fig. 2a, b), and (3) social preferences were independent of habitat complexity (i.e. they continued to be found in all complexity levels, as well as when using the more general GAI with association indices that combined all contexts; Fig. 2c, d).

Moreover, the distribution of high social affiliations (GAI >2.0) among individuals in the networks comprising all behavioural contexts resembled the ones during forage (Fig. 3a, b) better than travel and rest (Fig. 3c, d). In the population under lower disturbance, the proportion of strong social affiliation was higher (i.e. network connectance, $C = 0.065$) and the affiliation network showed stronger tendencies to be assorted by sex ($r_d^w \pm$ SE = 0.19 ± 0.07) and age classes (r_d^w ± SE = 0.11 ± 0.05) during forage than during travel or rest (see full results of network metrics in Appendix Table A6). In contrast, in the population under higher disturbance, the proportion of strong social affiliation was higher ($C = 0.066$) and the affiliation networks were prominently more assorted by gregariousness during travel (r_c^w ± SE = 0.82 ± 0.07) than during forage or rest (Appendix Table A6). Across the habitat complexity levels, the distribution of high affiliation values among individuals in all habitats combined most closely resembled those in the medium complexity habitat (Fig. 3e–h). Indeed, the affiliation networks of both populations were denser in habitats of medium complexity and showed a general trend of being assorted by sex, age or gregariousness in habitats with higher structural complexity (Appendix Table A6).

<H1>DISCUSSION

By controlling for multiple factors that bring individuals into groups, we found that social association patterns of giraffes vary by behavioural state. Contrary to our original hypotheses, individuals exhibited association preferences when foraging, with minor influences of habitat complexity and levels of disturbance. Furthermore, giraffes did not seem to have preferential associations while resting or travelling. Fission–fusion systems are adaptive responses to varying ecological conditions; individuals respond to real-time changes in both ecological and social conditions by frequently leaving or joining groups of conspecifics. Such plasticity is a critical component of behaviour that allows individuals to optimize their fitness and adapt to changing conditions (DeWitt, Sih, & Wilson, 1998). While individuals control the way they use the environment, the resulting association patterns contribute to emergent social structure, which is inherently adaptive (Bolnick et al., 2003; Saltz, Geiger, Anderson, Johnson, & Marren, 2016). By assorting behaviourally, individuals align themselves with others that have the same requirements as themselves, thereby potentially aligning motivation and avoiding conflict (Webber & Vander Wal, 2018).

Association indices are convenient tools for converting observations of individual animals in groups into a measure of their propensity to socialize (Cairns & Schwager, 1987; Whitehead, 2008). Assuming, quite reasonably, that grouping sets the stage for social interactions to occur (Whitehead & Dufault, 1999), such indices are widely used to portray and test social patterns across animal taxa (Farine & Whitehead, 2015; Whitehead, 2008). However, the literal translation of this metric—the proportion of time individuals were seen together—is subjected to sampling biases (Hoppitt & Farine, 2018; Weko, 2018) and overlooks the multiple underlying factors that can cause aggregation (Whitehead & James, 2015). We show that a coarse association measure (HWI) would suggest prevalent social preferences among individual

giraffes; that is, many pairs of individuals spend high proportions of time together. However, the more refined social measures presented here—which removed the effects of sex, age and gregariousness and accounted for behavioural and habitat contexts—show how such a conclusion would be premature. Rather, they reveal that giraffe social preferences are linked predominantly with foraging, strengthening the case that all-inclusive metrics of social relationships, such as association indices, can be too coarse (Castles et al., 2014; Farine & Whitehead, 2015) and may conceal true individual social preferences (Whitehead & James, 2015).

Since giraffes do not seem to have preferential associations while resting or travelling, the social preferences found here may be driven by females' selection of foraging companions that share the same requirements. Social structure in giraffes can contain multiple levels (VanderWaal, Wang, et al., 2014), and the age and sex of the nearest neighbour in a group of giraffes regulates the vigilance and foraging behaviour of other group members (Cameron & du Toit, 2005). Neither males nor females alter their vigilance scanning behaviour in relation to group size, but females spend significantly more time scanning their environment when their nearest neighbour is an adult bull, and smaller males spend more time scanning when in the presence of larger males (Cameron & du Toit, 2005). This increased vigilance cost (and consequent disruption of foraging behaviour) to females when in groups with adult males suggests that giraffes may modify their association choices depending on motivations and behavioural context. Female giraffes prefer herds with other females and related individuals (Bercovitch & Berry, 2013), which would appear to support the hypothesis that being in a group with adult males incurs increased vigilance costs and reduced foraging opportunities for adult females (Cameron & du Toit, 2005). In our case, the affiliation networks of foraging giraffes

tended to be more assorted by sex and age classes, further suggesting that adult females may associate with other females that also want to forage, and so avoid foraging with males, as it is too costly.

We also found that such social preferences among giraffes are somewhat influenced, yet not driven, by habitat settings and levels of disturbance. Habitat can influence social connectivity in both gregarious and nongregarious species in different ways. For instance, wolves, *Canis lupus,* respond to changes in habitat types by altering their territory size but not their pack size; by residing in habitats favoured by moose, *Alces alces,* a locally important prey species, wolves are able to maintain their pack size and reduce territory size, i.e. trade off the costs associated with maintaining a large territory with the benefits of accessing high prey density (Kittle et al., 2015). Maintaining large group sizes is correlated with time spent in the highest-quality habitats, thereby improving fitness; this is true for lions (Mosser, 2008; Mosser & Packer, 2009; VanderWaal, Mosser, & Packer, 2009) and European badgers, *Meles meles* (Kruuk & Parish, 1982). Furthermore, emigration from groups occurs when competition for resources exceeds the capacity of the habitat (Bowler & Benton, 2005; VanderWaal et al., 2009). Consequently, higher-quality habitats support larger group sizes and facilitate social aggregation.

We found that, in giraffes, there is a tendency for greater social connectivity and assortativity towards more physically structured habitats, but we also found that individuals showed consistently high affiliations independently of the habitat complexity level and physiognomy. Alone, the variation in habitat complexity in our study areas does not seem sufficiently marked to either disrupt or promote social grouping in giraffes. This reinforces that giraffe social patterns are structured by multiple drivers (e.g. VanderWaal, Wang, et al., 2014) and our findings suggest that their social preferences are firm enough that individuals keep

associating with their preferred companions across habitats ranging from open areas to dense woodlands. It is possible that the habitats in our study site were not sufficiently complex to influence association patterns. However, it is also possible that, for giraffes, habitat complexity does not have a big influence on group dynamics, since they are highly visible to each other (and presumably, predators) regardless of habitat complexity.

Moreover, the influence of habitat on social behaviour is expected to interact with disturbance levels (Orpwood, Magurran, Armstrong, & Griffiths, 2008) if more complex habitats decrease predator efficiency by providing refuge or escape routes for prey (see Warfe & Barmuta, 2004). Thus, one could expect higher social clustering in habitats with low complexity if social grouping is mainly a strategy to seek cover behind other group members (Orpwood et al., 2008). For instance, guppies, *Poecilia reticulata,* remain in groups for longer and maintain more and stronger associates in their social networks under high risk of disturbance (through predation) than in low-risk situations (Kelley, Morrell, Inskip, Krause, & Croft, 2011). Our findings suggest that levels of disturbance are unlikely to have such a strong influence on social preferences in giraffes, although it could still explain the different distribution of social preferences between the two populations. In the area with no lions or tourists (SC), the giraffe social affiliation networks were more assorted by sex and age and were denser when individuals were foraging; in the area where lions and high volumes of tourist traffic were present (LNNP), the networks were more assorted by gregariousness and were denser when travelling. However, giraffe females congregate when they have calves and when they engage in alloparental care (Dagg & Foster, 1976; Gloneková, Brandlová, & Pluháček, 2016; Horwich, Kitchen, Wangel, & Ruthe, 1983; Langman, 1977; Leuthold, 1979; Leuthold & Leuthold, 1978; Pratt & Anderson, 1979, 1985), and so the higher proportion of juveniles in the population under lower disturbance

may have contributed to stronger affiliations between females with calves. Under higher levels of disturbance there may be advantages of being socially closer, such as travelling with preferred companions, so whether the patterns we found represent passive or active assortments in giraffes remains an open question.

In line with our broader understanding of multilevel societies, our results contribute evidence that animals are capable of aligning their behavioural tactics in response to the socioecological environment (Webber & Vander Wal, 2018). A number of species are able to use behavioural cues when selecting habitat and vice versa; for example, least flycatchers, *Empidonax minimus,* choose habitat types based on the social information provided by others (Fletcher, 2009); in great tits, *Parus major,* populations are influenced by social learning that persists across generations (Aplin et al., 2015). In sleepy lizards, *Tiliqua rugosa,* increasing habitat structural complexity resulted in denser social networks but also an increase in aggression, suggesting that there was an optimal density at which the costs of being social began to outweigh the benefits (Leu et al., 2016). Our results contribute to the discussion of how the interaction between habitat and behaviour acts as a mechanism structuring animal societies and provides evidence that habitat and behavioural state may influence the formation of multilevel hierarchical social structure in a large fission–fusion species of mammal.

<H2>Conclusions

In many social species, simple measures of association have been used to demonstrate nonrandom associations, often interpreted as social preferences, 'friendships' or 'bonds' (Bercovitch & Berry, 2013; Carter, Seddon, et al., 2013; Chilvers & Corkeron, 2002; Deecke,

Barrett-Lennard, Spong, & Ford, 2010; Malyjurkova et al., 2014; Wiszniewski, Allen, & Möller, 2009). We have shown empirically that such measures of association may not capture the intricate and nuanced nature of animal relationships, as they lump together interactions observed in many behavioural contexts during which individuals may have different motivations to socialize. The context-dependent social preferences we identified in Rothschild's giraffes suggest that when foraging it may be relevant for individuals to be surrounded by their preferred associates—and we could speculate it is because these can be reliably vigilant or good at finding quality food patches. On the other hand, when giraffes are resting or on the move, it seems more important to be part of a group to, say, avoid predation, but it does not matter much which conspecifics they are with.

Although our sample size of two population networks may be viewed as limited, logistical constraints makes replication rare in studies of wild animal social networks; general conclusions about the social structure of a species is typically based upon single-population studies. Our approach highlights the nongeneralizability of single-network studies and we emphasize this element of our study design so that the results can be interpreted in the correct context. Finally, our study highlights how the consideration of social and asocial confounding factors can add to the granularity of detail that can be extracted from studies of social organization, over and above the use of traditional simple association measures. We hope our results shed light on the complex and multilayered nature of giraffe social behaviour and encourage a wider use of more detailed measures of social affiliation in portraying social organization of wild animals.

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Appendix

Table A1

Multiple quadratic regression assignment procedure (MRQAP) to evaluate how close-proximity associations (measured as half-weight association index, HWI) of Rothschild's giraffes in two Kenyan populations (Soysambu Conservancy, SC; Lake Nakuru National Park, LNNP) may be affected by context-dependent association matrices (behavioural states: forage, travel, rest), habitat complexity levels (low, medium, high) and individual covariates (sex, age class, gregariousness)

Dependent variable	Independent structural variables	SC population, lower disturbance		LNNP population, higher disturbance	
		Partial correlation	*P*	Partial correlation	*P*
HWI~	HWI forage	0.8840*	<0.001	0.9559*	<0.001
	HWI travel	0.5908*	<0.001	0.7330*	<0.001
	HWI rest	0.6460*	<0.001	0.8552*	<0.001
	Age	0.0315	0.2960	-0.1058*	0.0280
	Sex	0.1155*	0.0020	0.0201	0.4880
	Gregariousness	0.2243*	0.0020	0.0931	0.0660
HWI~	HWI low habitat	0.7644*	<0.001	0.9239*	<0.001
	HWI medium habitat	0.9088*	<0.001	0.9295*	<0.001
	HWI high habitat	0.8316*	<0.001	0.8181*	<0.001
	Age	0.0137	0.5200	0.0124	0.6940
	Sex	0.1007*	<0.001	0.0149	0.4040
	Gregariousness	0.0439	0.3020	0.0266	0.3720

Partial correlation is a measure of the effect size of a given predictor. Asterisks indicate statistical significance at the $\alpha = 0.05$ level using 1000 permutations.

Table A2

Multiple quadratic regression assignment procedure (MRQAP) to evaluate how the context-dependent close-proximity associations (half-weight association index, HWI) of Rothschild's giraffes in two Kenyan populations (Soysambu Conservancy, SC; Lake Nakuru National Park, LNNP) may be affected by structural variables depicting individual covariates (sex, age class, gregariousness)

Context-dependent variable	Predictors	SC population, lower disturbance		LNNP population, higher disturbance	
		Partial correlation	*P*	Partial correlation	*P*
Behavioural state					
HWI all~	Age	0.2632*	<0.001	0.0325	0.1800
	Sex	0.1829*	<0.001	0.3248*	<0.001
	Gregariousness	0.4338*	<0.001	0.4975*	<0.001
HWI forage~	Age	0.2697*	<0.001	0.0499	0.1300
	Sex	0.1517*	0.0020	0.3196*	<0.001
	Gregariousness	0.3540*	<0.001	0.4646*	<0.001
HWI travel~	Age	0.1656*	<0.001	0.0769	0.0880
	Sex	0.1215*	0.0040	0.1656*	0.0020
	Gregariousness	0.2330*	<0.001	0.0500	0.3380
HWI resting~	Age	0.0859*	0.0080	-0.0002	0.9900
	Sex	0.0329	0.2020	0.1310*	0.0040
	Gregariousness	0.2552*	<0.001	0.3770*	<0.001
Habitat complexity					
HWI all~	Age	0.3239*	<0.001	-0.0181	0.2020
	Sex	0.2654*	<0.001	0.3237*	<0.001
	Gregariousness	0.3067*	<0.001	0.3969*	<0.001
HWI low~	Age	0.2014*	<0.001	-0.0192	0.4960
	Sex	0.2580*	<0.001	0.2924*	<0.001
	Gregariousness	0.1662*	<0.001	0.3367*	<0.001
HWI medium~	Age	0.3005*	<0.001	0.0160	0.4460
	Sex	0.1716*	<0.001	0.2131*	<0.001
	Gregariousness	0.3516*	<0.001	0.3044*	<0.001
HWI high~	Age	0.2562*	<0.001	-0.0586	0.0620
	Sex	0.1907*	<0.001	0.2159*	<0.001
	Gregariousness	0.1277*	0.0040	0.2312*	<0.001

Partial correlation is a measure of the effect size a given predictor. Asterisks indicate statistical significance at the $\alpha = 0.05$ level using 1000 permutations.

Table A3

Permutation tests comparing the observed mean and standard deviation (SD) of social affiliation metrics (HWI, or generalized affiliation indices) with the mean and SD expected by chance (Random) after randomizing individual giraffes into pairs for 1000 iterations

	Context	Social affiliation metric	Observed mean	Random mean	*P*	Observed SD	Random SD	*P*
SC population, lower disturbance	All	HWI	0.175*	0.18	<0.001	0.155*	0.125	0.001
	Behaviour	HWIall~Age+Sex+Greg	-0.181*	-0.13	<0.001	1.364*	1.106	<0.001
		HWIforage~Age+Sex+Greg	-0.234*	-0.196	<0.001	1.253*	1.088	<0.001
		HWItravel~Age+Sex+Greg	-0.205	-0.204	0.286	0.959	0.96	0.577
		HWIrest~Age+Greg	-0.212	-0.21	0.253	0.99	0.995	0.758
	Habitat complexity	HWIall~Age+Sex+Greg	-0.193*	-0.142	<0.001	1.433*	1.144	0.001
		HWIlow~Age+Sex+Greg	-0.169	-0.167	0.115	0.951*	0.942	0.007
		HWImed~Age+Sex+Greg	-0.206*	-0.185	0.001	1.205*	1.099	<0.001
		HWIhigh~Age+Sex+Greg	-0.246*	-0.24	0.025	1.065*	1.048	0.019
LNNP population, higher disturbance	All	HWI	0.127*	0.13	0.001	0.118*	0.085	<0.001
	Behaviour	HWIall~Sex+Greg	-0.188*	-0.134	0.001	1.247*	1.031	0.001
		HWIforage~Sex+Greg	-0.201*	-0.178	0.003	1.124*	1.053	<0.001
		HWItravel~Sex	-0.214	-0.211	0.081	0.896	0.892	0.151
		HWIrest~Sex+Greg	-0.252	-0.233	0.01	0.947	0.943	0.369
	Habitat complexity	HWIall~Sex+Greg	-0.218*	-0.154	0.001	1.302*	1.046	<0.001
		HWIlow~Sex+Greg	-0.231*	-0.216	<0.001	1.042*	0.979	<0.001
		HWImed~Sex+Greg	-0.253	-0.245	0.053	1.080*	1.017	<0.001
		HWIhigh~Sex+Greg	-0.223	-0.232	0.998	0.888*	0.874	0.016

SC: Soysambu Conservancy; LNNP: Lake Nakuru National Park. GAI are the deviance-converted residuals of generalized linear models taking half-weight association index (HWI) as a function of the combination of following predictors: sex (male/female), age class (adult/bull/subadult/juvenile) and gregariousness (Greg). The association matrices were context dependent: behavioural context (forage/travel/rest)

and habitat complexity level (low, medium, high). Note that the predictors of each GAI were selected after the MRQAP analyses in Table A2. Asterisks indicate statistical significance at the $\alpha = 0.05$ level using 1000 permutations.

Table A4

Number of individuals in each sex and age classes used in each contextual analysis

Population	Context	Total	Sex			Age			
			Female	Male	Immature	Adult	Mature bull	Subadult	Juvenile
SC	Behavioural state	55	31	24	0	21	5	13	16
	Habitat complexity	65	32	33	0	21	7	21	16
LNNP	Behavioural state	45	19	26	0	31	7	7	0
	Habitat complexity	76	40	36	0	54	9	13	0

SC: Soysambu Conservancy; LNNP: Lake Nakuru National Park.

Table A5

Comparisons of mean generalized affiliation indices (GAI) of each population (Soysambu Conservancy, SC; Lake Nakuru National Park, LNNP) in each context (behavioural state, habitat complexity) using two-tailed two-sample Kolmogorov–Smirnov tests

	SC, lower disturbance		LNNP, higher disturbance	
	D	*P*	*D*	*P*
Behavioural state	**All states**		**All states**	
Forage	0.012	0.999	0.076	0.1025
Travel	0.248**	4.16×10^{-14}	0.199**	2.99×10^{-9}
Rest	0.189**	2.09×10^{-8}	0.146**	$3.39*10^{-5}$
Habitat complexity	**All habitats**		**All habitats**	
Low	0.348**	2.20×10^{-16}	0.283**	2.20×10^{-16}
Medium	0.068	0.183	0.098*	0.015
High	0.269**	2.20×10^{-16}	0.252**	1.53×10^{-14}

P values refer to pairwise comparison between the distribution of GAI in all behavioural states (all states) versus each state separately (forage, travel, rest) and the distribution of all habitat complexities (all habitats) versus each complexity level separately (low, medium, high). *$P < 0.05$; **$P < 0.001$. The Kolmogorov–Smirnov tests suggest that in both giraffe populations the distribution of GAI when considering data from all behavioural states differed from the distribution of GAI when individuals were travelling and resting but not when they were foraging. The tests also suggest that the distribution of GAI when considering data from all habitat complexities differed from the distribution of GAI when individuals were in habitats with low and high complexity levels but not when they were in habitat with medium complexity (note the latter was not true for the population under higher disturbance).

Table A6

Global metrics for the context-dependent social affiliation networks of two populations of Rothschild's giraffes, one under lower disturbance (Soysambu Conservancy, SC) and another under higher disturbance (Lake Nakuru National Park, LNNP)

Metric	Behavioural state			Habitat complexity		
		SC, lower disturbance	LNNP, higher disturbance		SC, lower disturbance	LNNP, distur
Connectance	**All**	0.079	0.058	**All**	0.077	0.074
	Forage	**0.065**	0.039	Low	0.017	0.040
	Travel	0.029	**0.066**	Medium	**0.055**	**0.050**
	Rest	0.041	0.039	High	**0.055**	0.031
Assortativity by sex classes	**All**	0.334±0.066	0.443±0.089	**All**	0.002±0.059	0.195
	Forage	**0.190±0.073**	0.362±0.112	Low	-0.249±0.115	0.109
	Travel	0.068±0.111	0.138±0.092	Medium	0.075±0.069	**0.182**
	Rest	0.121±0.093	**0.416±0.103**	High	**0.091±0.067**	0.149
Assortativity by age classes	**All**	0.149±0.048	0.012±0.085	**All**	-0.003±0.038	0.156
	Forage	**0.106±0.049**	**0.101±0.128**	Low	-0.148±0.068	0.061
	Travel	-0.005±0.066	-0.058±0.057	Medium	-0.048±0.043	0.023
	Rest	0.087±0.062	-0.130±0.084	High	**0.012±0.042**	**0.084**
Assortativity by gregariousness	**All**	0.217±0.061	0.396±0.084	**All**	0.074±0.053	0.260
	Forage	0.239±0.071	0.221±0.113	Low	0.225±0.097	0.280
	Travel	**0.491±0.082**	**0.816±0.066**	Medium	0.436±0.054	0.379
	Rest	0.461±0.113	0.540±0.076	High	**0.527±0.044**	**0.595**

Networks were defined by individual giraffes connected by edges representing high social affiliations (generalized affiliation indices >2.0) that are indicative of social preferences, in different contexts: behavioural states (all, forage, travel, rest) and habitat complexity (all, low, medium, high). Connectance is a measure of connectivity and was quantified as the proportion of realized links in the network. Assortativity measures the tendency for individuals to cluster according to a discrete or a continuous variable—here sex (male, female), age (adult, big bull, juvenile, subadult), and gregariousness—quantified by weighted assortativity indices (± standard error estimated by jackknife). Values in bold denote the highest positive value in each behavioural and habitat context.

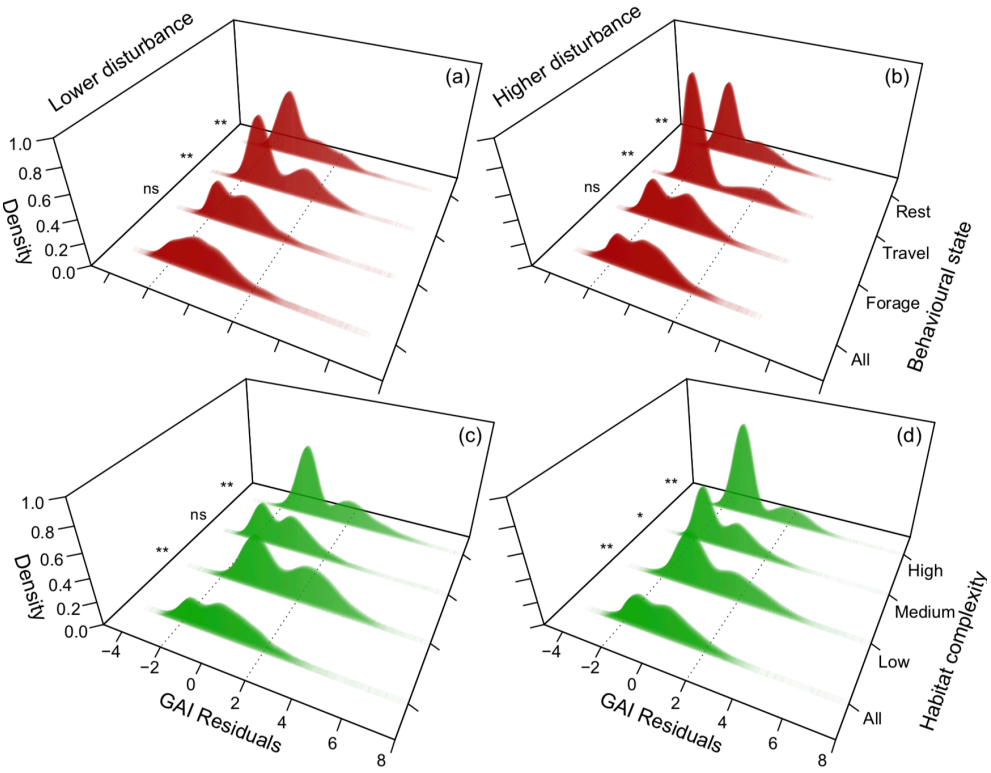

Figure 1. Context-dependent social affiliations in Rothschild's giraffes. Kernel density estimation of generalized affiliation indices (GAI) across contexts and populations (*Z* axis). GAIs are the deviance-converted residuals (*X* axis) of generalized linear models between context-dependent association matrices and structural variables representing individual covariates (*Y* axis, Appendix Tables A2, A3). Rows display the distribution of social affiliations in different contexts: (a, b) behavioural states and (c, d) habitat complexity levels. Columns represent populations under lower (SC) and higher (LNNP) disturbance. Dashed lines are indicative of the thresholds beyond which there is evidence of positive affiliation (social preference: GAI >2.0) and negative affiliation (social avoidance GAI <-2.0). The significance of the two-sample Kolmogorov–Smirnov comparisons between the GAI distribution in all behavioural states and habitat complexities (All) and with each state and complexity level separately (*$P < 0.05$; **$P < 0.001$) (see Appendix Table A5).

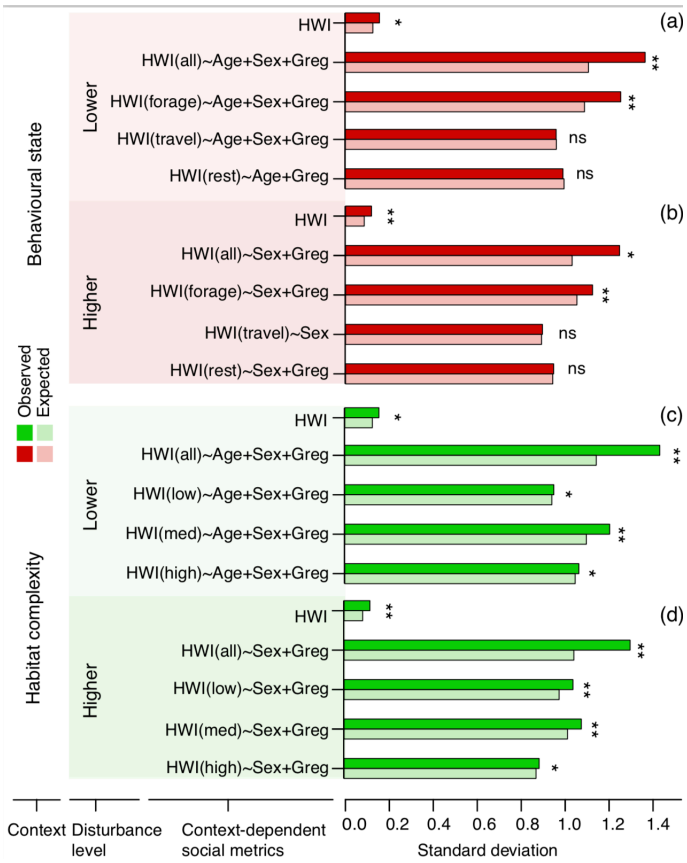

Figure 2. Testing the null hypothesis of random associations among individual giraffes in different contexts. Results of Monte Carlo permutation tests comparing the empirical standard deviation (SD, *X* axis) of different context-dependent social metrics (*Y* axis) with the SD expected by chance after randomizing individual giraffes into groups. Evidence for social preferences (unusually high social metric values) and avoidances (unusually low values) are indicated by a significantly higher SD of the observed data (darker bars) relative to random SD (respective lighter bars). $*P < 0.05$; $**P < 0.001$. Social metrics were tested in different behavioural states (all/forage/travel/rest) and habitat complexities (all/low/medium/high) for a population under lower disturbance (SC) and another under higher disturbance (LNNP). Tested social metrics included the half-weight index (HWI) and customized generalized affiliation indices (GAI), which are the residuals of linear models taking HWI as a function of the structural predictors sex (male/female), age (juvenile/subadult/adult/big bull) and gregariousness. Predictors for each GAI were selected via MRQAP (Appendix Tables A1, A2); for all test details see Appendix Table A3.

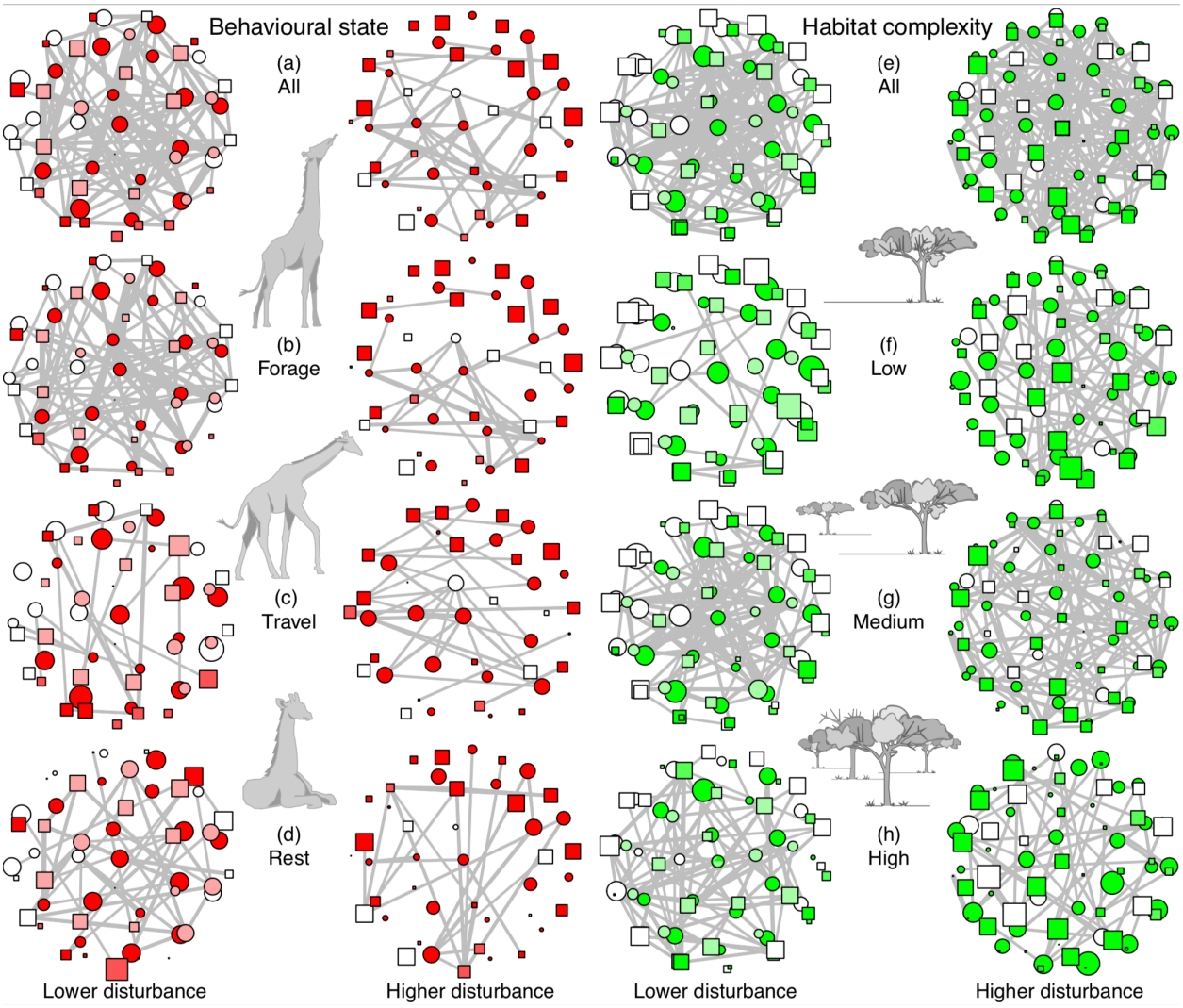

Figure 3. Context-dependent social affiliation networks in Rothschild's giraffes. Each network indicates social preferences among individuals in a different context. Behavioural states in red: (a) all, (b) forage, (c) travel, (d) rest; and habitat complexity in green: (e) all, (f) low, (g) medium, (h) high. Columns in each context represent a population under lower (SC) and higher (LNNP) levels of disturbance. Nodes representing individuals are differentiated by sex (circle = female; square = male), age (colour shade from darkest to white = adult, old bull, juvenile, subadult) and size (proportional to gregariousness), and are connected by edges whose thicknesses are proportional to their GAI values (deviance residuals of models in Fig. 2). To depict social preferences, only GAI >2.0 are shown; for visual comparison, individuals of the same population are plotted in the same spatial coordinates across contexts.